

A study of *Bixa* (Bixaceae), with particular reference to the leaf undersurface indumentum as a diagnostic character

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SYNOPSIS. In the course of preparation of an account of Panamanian *Bixa urucurana* Willd. for the *Seedling Flora Project*, differences in leaf undersurface indumentum were found between adults and juveniles. We describe the pattern of variation of indumentum between species within the genus and between developmental stages within *B. urucurana*. We conclude that leaf undersurface indumentum is a useful diagnostic character for the adult stages of the genus but not the juvenile stages.

INTRODUCTION

Bixa is the only genus of the small woody family, Bixaceae which is widespread in tropical America and frequently cultivated throughout the tropics. The genus has often been treated as one highly variable species, *Bixa orellana* L. sensu lato (Eichler, 1871; Kuntze, 1891; Warburg, 1895; Standley & Williams, 1961; Robyns, 1967; Croat, 1978) or as five separate species (Macbride, 1941; Baer, 1976; Molau, 1983). Primarily fruit and indumentum characters have been used to distinguish different species. Linnaeus' (1753) protologue of *B. orellana* simply described the capsules as 'chestnut-like'. Willdenow (1809) described a second species, *B. urucurana* from Brazil, defining it by the 'white' scales densely covering the leaf underside. This species has frequently been reduced in rank to a variety of *B. orellana*, especially in Central America (Kuntze, 1891; Standley & Williams, 1961; Robyns, 1967). In 1831, Don published a description of *B. platycarpa* Ruiz & Pav. from Peru, which had flat, kidney-shaped fruits with very few bristles. Triana (1858) described *B. sphaerocarpa* from Nouvelle-Grenade (now Colombia), having scaly leaf undersides and spherical capsules, but this was later reduced to a synonym of *B. urucurana* (Pilger, 1925; Baer, 1976). Huber (1910) described *B. arborea*, having a kidney-shaped, dorsally compressed capsule with a wrinkled surface. Finally, *B. excelsa* Gleason & Krukoff was described in Gleason (1934), and is characterized by reniform capsules densely covered by glandular trichomes. Although the original descriptions of the three species restricted to the Amazon basin (*B. arborea*, *B. excelsa*, *B. platycarpa*) all refer to a

more or less kidney-shaped fruit, there are other defining features which separate them as species. Baer (1976) contends that they are diagnosable on fruit shape when this is more accurately defined. Other diagnostic characters include fruit ornamentation, dehiscence, life-form, and the size and density of trichomes on the undersurface of the leaf (see Table 1 for a summary of these).

The primary taxonomic difficulty in the genus is separating *Bixa orellana* and *B. urucurana*. There is a high degree of variation between cultivars of *B. orellana*, especially in capsule shape since this has been the subject of artificial selection. Baer (1976) discusses possible intermediates or hybrids between *B. orellana* and *B. urucurana*, known predominantly from Panama and Costa Rica. These apparently have trichomes of intermediate size and density, relatively short, subspherical fruits with slender spines and intermediate numbers of seeds.

The variation in leaf indumentum is our principal concern. The undersurfaces of leaves of all five species of *Bixa* have peltate scales, which are circular discs supported on short obconical stalks about 20 µm long. They are red-brown in colour and formed of an outer ring of cells with a central circular area which is more densely pigmented. In *B. urucurana*, the scales are large, with several concentric rings of cells around the central core, irregular in outline and funneliform. Its scales are also very densely packed, giving a tawny-brown appearance to the undersurface of the leaf. (Willdenow's (1809) original description of white scales probably referred to a shiny appearance, observed due to reflection of incident light at certain angles).

Our study is based on herbarium material collected and

Table 1 Summary of life form, fruit and scale characters of the five *Bixa* species. (Baer, 1976; Molau, 1983; Macbride, 1941)

Species	Fruit shape		Spines	Dehiscence	Habit	Trichome	
	l.s.	t.s.				diameter (μm)	density (per mm^2)
<i>B. arborea</i>	subreniform	circular	absent	D	tree	69	12
<i>B. excelsa</i>	oblate	circular	stout, with glandular pubescence	D	tree	54	6
<i>B. orellana</i>	oblate/cordate	circular	absent or slender	D	shrub	64	19
<i>B. platycarpa</i>	circular	flat	absent	D	tree	63	50
<i>B. urucurana</i>	circular/depressed oblate	circular	tapered	I	shrub	94	156
<i>B. 'intermediates'</i>	oblate	circular	slender	D	shrub	80	59

Dehiscence: D= dehiscent, I= indehiscent. Trees are above 30 m at maturity, shrubby species grow to about 10 m. Trichome diameter is a mean (n unknown) and density 'representative' (taken from Baer, 1976).

grown in Panama for the *Seedling Flora Project* (see Garwood & Humphries, 1993). Accessions from this area have often been attributed to *Bixa orellana* L. sensu lato (Robyns, 1967; Croat, 1978). Our adult collections seem to refer to *B. urucurana* on the basis of both fruit and indumentum characters. However, we observed fewer and smaller scales on juvenile stages of the progeny of this adult (see description in Garwood, 1994) and felt that these observations merited further investigation. We pursued three main lines of enquiry: A) Within *B. urucurana*, are there significant differences in scale diameter and density at different positions across the lamina of the leaf or between different stages of development? How is variation in scale diameter apportioned between the central core and outer annulus of the scale? B) Do differences in scale density and diameter within juvenile individuals follow any trends associated with either leaf node or size? and C) How much variation in scale density and diameter is there between adults of the five different species of *Bixa* across their geographical range and is there any evidence for the existence of intermediates between *B. orellana* and *B. urucurana*?

MATERIALS AND METHODS

Seeds were collected from one individual of *Bixa urucurana* along the Chagres River, Gamboa, Panama in May 1986 and April 1987. These seeds were germinated in a screened growing house on Barro Colorado Island (BCI), Panama. The resulting juveniles were harvested at intervals and pressed to provide herbarium specimens of various stages of development. A voucher specimen was also collected of the adult in May 1986. Two *Bixa* seedlings were collected from a beach on BCI, but the parental seed source was unknown.

A) To determine whether significant variation occurred in *Bixa urucurana* in scale size and density between different positions on the lamina, and between stages of development, and to ascertain where scale diameter variation arises (whether central core or outer annulus), we took an initial sample of two leaves from each of five juveniles and one of the beach seedlings. This was also undertaken for two leaves of the adult voucher specimen. Scale density was measured as the number of scales per mm^2 with a photogratule on a Leica dissecting microscope. Ten measurements were made at each of three positions across the lamina; at the edge, in the middle and adjacent to the primary vein. Scale diameter was measured using an eyepiece graticule in a compound

microscope at $\times 125$ magnification. Small squares (about 1 mm^2) of leaf tissue cut from the three positions described above were placed on a glass slide and the diameter of both the dark, central portion and the entire scale were measured for ten scales at each position. The results were analyzed as follows: i) two-way (Model II) analysis of variance (ANOVA) was used to partition the variance in scale density, scale core diameter and total scale diameter into components attributable to lamina position, leaf and position \times leaf interaction effects. ii) three-level nested ANOVA (Model II) was employed to partition the three scale variables into the effects of stage, individual and leaf. Variance components were calculated by the methods of Sokal & Rohlf (1981). These results and those of the following investigations were all analyzed using SYSTAT (Wilkinson, 1990).

B) To determine whether variation in scale density and diameter varied with leaf node and size within an individual, two of the largest juveniles were further studied, repeating the above measurement procedures, for edges of leaves only, for all leaves available on the specimens. The leaf length and width and the node from which the leaf originated were recorded. From this data, means and standard errors were calculated for each variable at each node and the results plotted. Relationships between scale diameter, scale density, leaf node and width, were tested by a linear regression for multiple values of y per x: resulting regression mean squares were tested over the deviation mean square and the proportion of variance attributable to the linear regression was evaluated by the coefficient of determination (r^2) (Sokal & Rohlf, 1981). The relationship between leaf-length and width was quantified using the Pearson product-moment correlation coefficient (r).

C) To estimate the variation in scale size and density in the genus *Bixa* as a whole, a selection of specimens in the BM herbarium was chosen (see Appendix). Five edges of leaves were measured for scale density and diameter in the same manner as described above, for one leaf of each of the chosen specimens. Specimens of *B. orellana* from Central America, South America and the West Indies and *B. urucurana* from Central and South America, were chosen from those with reliable recent determinations or mature fruits. For the other three Amazonian species, all specimens with leaf undersurfaces uppermost were studied, including several type specimens, since little material was available. Mean scale density and mean total scale diameter were calculated for each of these specimens.

Table 2 Results of two-way ANOVA (Model II) of effects of position (edge, middle or vein) and leaf on scale density and diameter. Two leaves on each of five juveniles and one adult were included.

Source	DF	Scale diameter								Scale density			
		Total scale				Central core							
		MS	F	P	%	MS	F	P	%	MS	F	P	%
Leaf	11	254.23	221.07	***	91.00	3.05	3.70	**	12.76	6165.03	311.66	***	94.39
Position	2	2.94	2.55	ns	.16	.61	.74	ns	0.00	74.59	3.77	*	.21
Leaf * position	22	1.15	1.50	ns	.41	.82	1.75	*	6.08	19.78	1.83	**	.41
Error	324	.77			8.31	.47			81.16	10.82			4.98

DF, degrees of freedom; MS, mean squares; F, F-statistic; P, probability: *, $0.01 < p \leq 0.05$; **, $0.001 < p \leq 0.01$; ***, $p \leq 0.001$; ns, not significant; %, percent of total variance contributed by variance component of each source.

Table 3 Results of three-level nested ANOVA (Model II) for stage (adult vs juvenile), individuals within each stage, and leaves within individuals, of scale diameter and density.

Source	DF	Scale diameter								Scale density			
		Total scale				Central core							
		MS	F	P	%	MS	F	P	%	MS	F	P	%
Stage	1	913.90	253.65	***	96.11	3.01	1.41	ns	3.97	17184.20	48.45	**	88.55
Individual	4	3.60	1.16	ns	.08	2.13	3.92	**	13.03	367.66	.68	ns	0.00
Leaf	6	3.14	3.69	**	.81	.40	.72	ns	0.00	542.11	44.34	***	9.30
Error	108	.85			3.00	.55			83.01	12.23			2.15

DF, degrees of freedom; MS, mean squares; F, F-statistic; P, probability: *, $0.01 < p \leq 0.05$; **, $0.001 < p \leq 0.01$; ***, $p \leq 0.001$; ns, not significant; %, percent of total variance contributed by variance component of each source.

RESULTS

A) For scale density in *Bixa urucurana*, a two-way ANOVA (Table 2) indicated a significant effect of position, leaf and position \times leaf interaction. However, the greatest part of the variance is accounted for by differences between leaves (94%), and a very small portion is attributable to position on the lamina or the leaf \times position interaction. For total scale diameter, position and the interaction term are not significant, whilst most of the variation (91%) is again accounted for by differences between leaves. While leaf and leaf \times position interaction effects were significant, most of the variation (81%) in core diameter was among replicate scales on leaves. Since position did not appear to be an important effect, further sampling and analysis was carried out on the edge of the leaves only, as this was easier and caused less damage to the specimens.

The results of the three-level nested ANOVA are summarized in Table 3. There is significant variance in scale density and total scale diameter between adult and juvenile specimens of *Bixa urucurana*, and between leaves, but not between individuals. Most of the variation of total scale diameter (96%) and density (89%) is attributable to differences between adults and juveniles. The results for central core diameter are quite different. Only the difference between individuals is significant and most of the variation (83%) occurs within replicates on leaves. Since there was so

little variation in central core diameter, total scale diameter alone was used in further analyses.

B) The variation of scale density, scale diameter and leaf width with node for the two largest juveniles is shown in Fig. 1. Leaf age decreases with node number: because the youngest leaves at the highest nodes are still expanding they have a small width and a very high scale density and were excluded from the analysis. For fully expanded leaves, of both individuals, *Garwood* 1830D and *Garwood* 2085D, mean scale density increases with leaf node ($F_{(1,12)} = 6.601$, $p = 0.025$; $F_{(1,7)} = 41.730$, $p = 0.001$, respectively), although the linear regression accounts for only a proportion of the total variation ($r^2 = 0.244$ and 0.588 respectively). The increase in scale density is independent of leaf width: a linear regression of scale density on leaf width was not significant in either individual ($F_{(1,12)} = 0.794$, $p = 0.500$; and $F_{(1,7)} = 1.391$, $p = 0.500$). We tested only leaf width, because leaf length was highly correlated with width in both individuals ($r_{(12)} = 0.892$, $p = 0.001$; and $r_{(7)} = 0.916$, $p = 0.001$). Scale diameter does not appear to have any significant trend associated with leaf node or size in either individual ($F_{(1,12)} = 3.966$, $p = 0.100$ and $F_{(1,7)} = 0.633$, $p = 0.500$ for node; $F_{(1,12)} = 0.148$, $p = 0.250$ and $F_{(1,7)} = 0.005$, $p = 0.75$ for width) and the proportion of variation accounted for by the linear regression was very low ($r^2 \leq 0.039$ for node; $r^2 \leq 0.002$ for width). The leaf dimensions of our juvenile specimens (11.5–22.6 cm long \times 8.7–16.7 cm wide) exceeded the range of our adult speci-

mens (9.4–13.6 cm long \times 5.0–9.7 cm wide) and are well within the published ranges for adults of the species (5.5–27 cm long \times 3–18 cm wide), (Standley & Williams, 1961; Robyns, 1967; Molau, 1983).

C) *Bixa orellana* and *B. urucurana* have the least certain specific status in the genus. On a plot of mean scale diameter versus mean scale density (Fig. 2a) specimens attributable to these taxa cluster into two groups (see Appendix for list of specimens), the lower being *B. orellana* and the upper *B. urucurana*, with two exceptions. Firstly, the Panamanian Fendler 328 specimen ('F' in Fig. 2a), the BM specimen of which consists of a mature *B. urucurana* fruit and a separate small non-fruiting branch, clearly groups with *B. orellana*. Baer (1976) placed a specimen from the same collection in *B. urucurana*. Secondly, our juvenile specimens of *B. urucurana* from Panama and the unidentified *Bixa* sp. seedlings from BCI clearly group at the lower end of the *B. orellana* range. In contrast, the (adult) parent is clearly in the *B. urucurana* group.

South American specimens of both *Bixa orellana* and *B. urucurana* group at the extremes of the ranges of both mean scale diameter and density. The Central American specimens of both taxa group towards the centre of the overall range of indumentum characters. West Indian specimens of *B. orellana* group closely with South American representatives of the same taxon.

Although there are too few specimens to form a reliable cluster, the three Amazonian tree species (*B. arborea*, *B. excelsa* and *B. platycarpa*) also cluster with *Bixa orellana* (Fig. 2b).

DISCUSSION

There is considerable variation in the indumentum of leaf undersurfaces in the genus *Bixa*. There are also several different trends in this variation which need to be considered and explained before the utility of indumentum differences as a diagnostic character of species can be evaluated.

Differences between positions on the same leaf were found to be much less significant than other effects (e.g. leaf, individual or age) for scale density and not significant for scale diameter. Baer (1976) stated that scale density increased near veins or at the base of the leaf, but we found little evidence for this in either adults or juveniles.

Both scale density and scale diameter are radically different between adults and juvenile stages of *Bixa urucurana*. On average, adult scales are more than twice as large and about four times denser than those of the juveniles. There is a slight overlap, however, between the ranges of density in adults

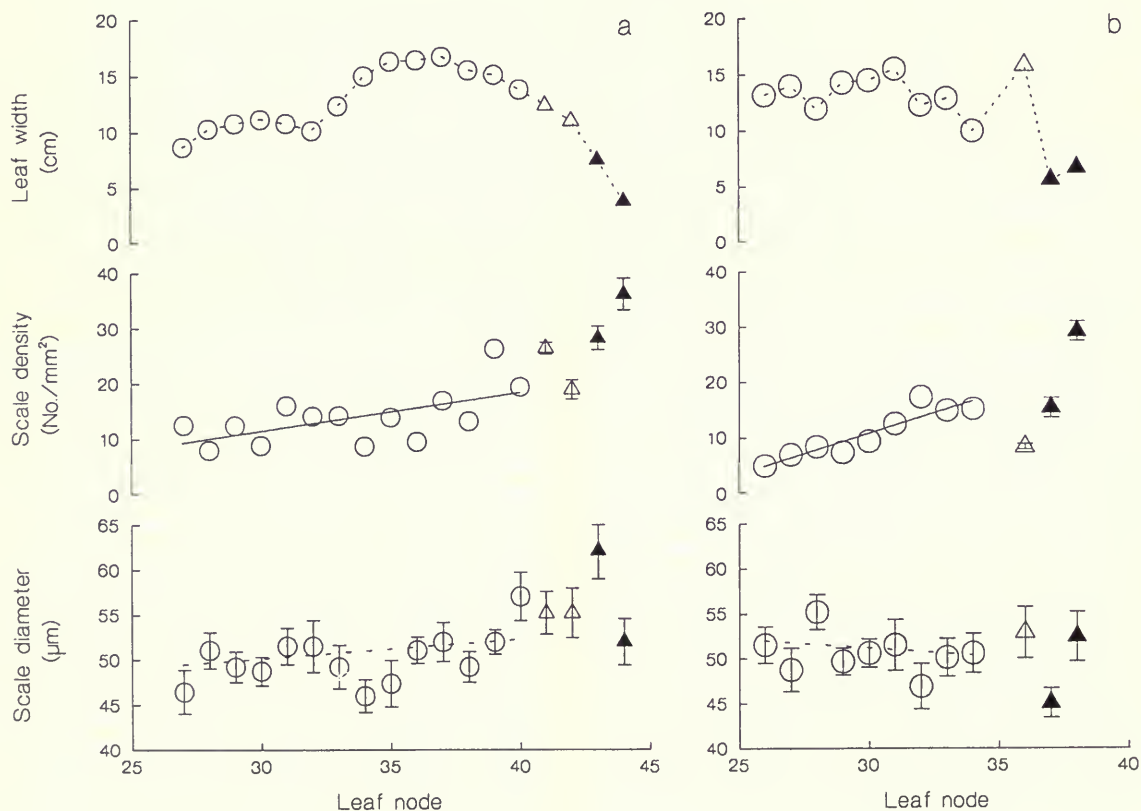


Fig. 1 Relationship of scale diameter, scale density and leaf width to leaf node in juvenile specimens.

(a) Juvenile Garwood 1830D.

(b) Juvenile Garwood 2085D.

(Open circles represent fully expanded leaves, filled triangles expanding leaves and open triangles 'borderline' leaves. Error bars for scale density and diameter represent the standard error of the mean and, where missing, the errors are smaller than the symbols. For scale diameter, the hatched line represents a non-significant linear regression. The linear regressions for scale density are significant ($p \leq 0.025$). Only fully-expanded leaves were included in the regression calculations.)

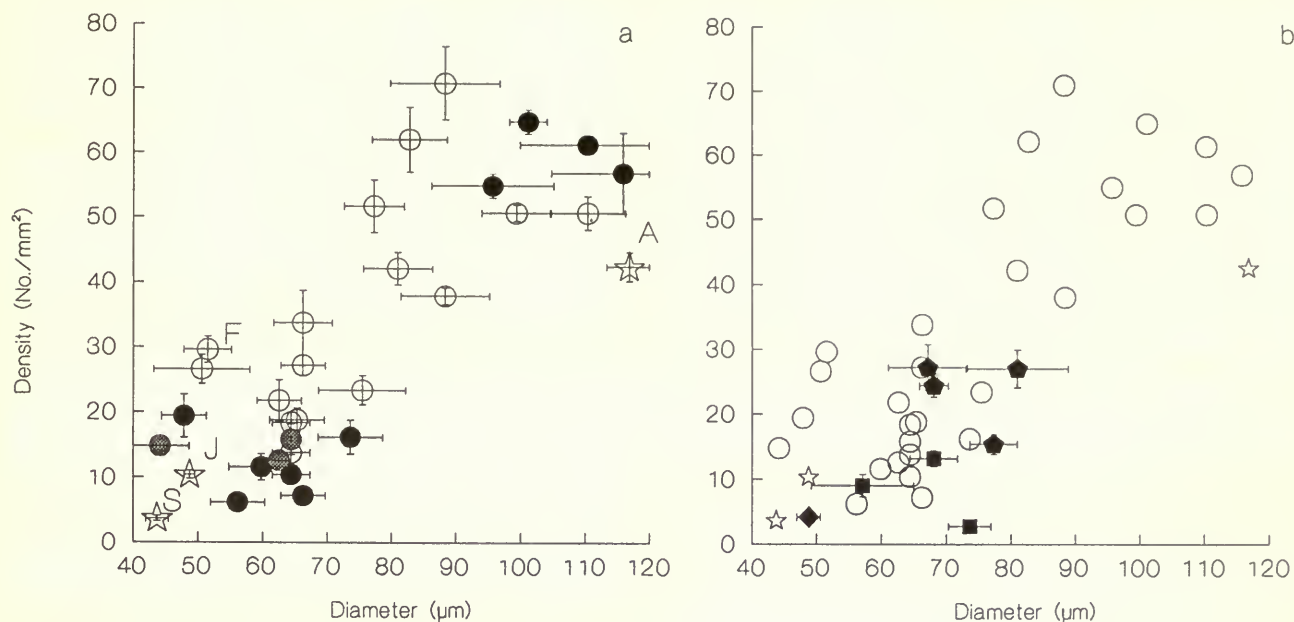


Fig. 2 Scale diameter versus scale density in *Bixa* spp. Mean \pm SE (N = 5 replicates on one leaf except for *Garwood* specimens marked by stars).

- (a) *B. orellana* and *B. urucurana*. (Filled circles represent South American collections, hatched circles West Indian collections and open circles Central American collections. Stars represent our Panamanian collections: A = Adult (N = 10 replicates from two leaves on one individual), J = Juvenile (N = 10 replicates from two leaves on each of five individuals) and S = *Bixa* sp. seedling (N = 10 replicates from two leaves on one individual). F = Panamanian specimen *Fendler* 328.
- (b) Five *Bixa* species. (Open circles and stars represent *B. orellana* and *B. urucurana* specimens from Fig. 2a; squares, *B. arborea*; pentagons, *B. platycarpa*; diamond, *B. excelsa*).

(27–65 scales per mm²) and juveniles (2–35 scales per mm²). There is no overlap between scale diameter of the juveniles (27.6–73.6 μ m) and the adults (82.8–147.2 μ m).

The difference in total scale diameter between adults and juveniles is accounted for by the outer portion or annulus of the scale: there is no significant difference in central core diameter between stages. In *Bixa urucurana*, the scales on adult leaves have a number of concentric rings of colourless cells around the dark central core (Baer 1976). Evidently, it is an increase in the number of these rings which increases overall scale size in the adults of this species. Although we observed these annuli in juvenile specimens, they were generally very narrow, comprising perhaps only one or two rings of cells and were occasionally completely absent, especially in the very young beach-collected seedlings.

The second trend within *Bixa urucurana* is that scale density increases with node number in juvenile specimens, whilst there is no clear trend in scale diameter with node number. However, since we found a significant difference in scale diameter between adults and juveniles, it would appear that changes in this parameter (i.e. the increase in number of rings of cells around the centre of the scale) must occur at some point between the two stages of plant development we studied. Further study of a range of intermediate, sapling stages would be required to ascertain whether there is a gradual increase in scale size with node. Scale diameter is not low due to small leaf size, since our juvenile leaves are generally larger than the adult leaves examined.

Thirdly, the comparison between our specimens and those of a sample from the BM herbarium shows that two distinct clusters of taxa are formed when mean scale diameter is

plotted against mean scale density (Fig. 2). The lower group with small, sparse scales includes all the specimens of *Bixa orellana* sensu stricto. The upper cluster of individuals with large, relatively densely packed scales, contains specimens which were originally variously identified as *B. orellana* sensu lato, *B. urucurana*, *B. orellana* var. *urucurana* or *B. sphaerocarpa* (see Appendix). We interpret these as *B. urucurana* since they form a close-knit group on the basis of indumentum characters and their fruit characteristics correspond, being subspherical, spiny and indehiscent. The problematic specimen, *Fendler* 328 ('F' on Fig. 2a) which Baer identified as *B. urucurana*, clearly groups with *B. orellana* on the basis of indumentum characters. However, there is a mature, subspherical capsule on the herbarium sheet which looks like that typical of *B. urucurana*. On closer inspection, it was noticed that the vegetative shoot on the herbarium sheet was non-reproductive and had never borne flowers or fruit; therefore, it must have been collected either from a completely different part of the same plant or even perhaps from a different individual than the fruit.

The South American specimens of the two shrubby species, *Bixa orellana* and *B. urucurana*, group at the extremes of the range of indumentum characters (Fig. 2a). Although the Central American specimens still form recognizable clusters with the conspecific specimens from South America, their indumentum characters tend to fall into the middle of the overall range for the two species. It would appear from Baer's (1976) estimates of scale density and diameter (Table 1) that some of the Central American specimens fall into his 'intermediate' category. However, his scale density estimate for *B. urucurana*, 156/mm², is inordinately high when compared to

our measurements: our highest mean value was 70 scales/mm² and our highest single value was 85 scales/mm². Unfortunately, because Baer does not give his sample sizes, it is difficult to compare the measurements. The fact that specimens of the two Central American species are much closer to each other than are those from South America, may suggest that there is some degree of intermediacy. Perhaps if we had sampled more specimens, we would have observed more of a continuum rather than two separate clusters. Since West Indian specimens of *B. orellana* group with South American specimens of the same taxon, it appears that dispersal (either naturally or through cultivation) has taken place directly from South America to the West Indies, bypassing Central America.

We conclude that the differences between indumentum characters in *B. orellana* and *B. urucurana* adults distinguish them as two separate species. This is reinforced by differences in fruit characters (see Table 1).

The three Amazonian tree species cluster with *Bixa orellana* and do not appear to be separable from it on the basis of indumentum characters alone, although it is recognized that the sample studied here is small.

It is apparent that *Bixa urucurana* manifests a broad range of scale diameter and density as it proceeds through its

development. The stages in this process apparently encompass all the variation observed in *B. orellana* and the Amazonian species. That four of the five *Bixa* species and the juveniles of *B. urucurana* have small sparse scales suggests that perhaps the large, densely packed scales of adult *B. urucurana* represent a more derived state.

The demonstration of the range of variation in indumentum characters through development within *Bixa urucurana* clearly shows that the utmost caution must be exercised when using them as diagnostic characters within the genus. It is important primarily to ensure that the leaf material studied comes from a mature individual.

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APPENDIX

Table of specimens examined.

Species	Collector(s)	No.	Country	Original ID	Later ID	Mean (SEM)	
						Scale density (No./mm ²)	Scale diameter (μm)
<i>B. arborea</i>	Ducke	8311	Brazil	A		13 (1.2)	68 (3.7)
	Huber	7827	Brazil	A		3 (1.0)	74 (3.3)
	Krukoff	8551	Brazil	A	A (DB '76)	9 (1.7)	57 (7.9)
<i>B. excelsa</i>	Krukoff	6831	Brazil	E		4 (0.5)	49 (1.8)
<i>B. orellana</i>	Barclay	425	Ecuador	O	O (UM '82)	10 (1.2)	64 (2.9)
	Barclay	851	Colombia	O	O (UM '82)	6 (1.3)	56 (4.2)
	Bunting & Licht	1070	Nicaragua	O		26 (2.2)	51 (7.4)
	Hahn	104	Martinique	O		15 (0.5)	44 (4.5)
	Hall & Bockus	7849	Colombia	OO		27 (1.6)	66 (3.4)
	Hartman	12006	Panama	O	O (RL '84)	19 (1.8)	65 (4.2)
	Jenman	5268	British Guiana	O		7 (0.8)	66 (3.4)
	Mexia	6435	Peru	O	O (UM '82)	16 (2.6)	74 (5.0)
	Nelson & Vargas	5072	Honduras	O	O (RL '91)	33 (4.9)	6 (4.5)
	Saunders	694	Honduras	O		23 (2.2)	75 (6.8)
	Tenorio & Miller	3313	Mexico	O	O (FR '83)	21 (3.1)	63 (3.4)
	Wagner	519	Puerto Rico	O		12 (0.8)	63 (1.8)
	Whitefoord	3169	Belize	O		18 (1.6)	64 (2.9)
	Whitefoord	4592	Dominica	O		16 (2.3)	64 (0.0)
	Williams	579	Bolivia	O		11 (2.0)	60 (5.0)
	Williams	649	Bolivia	O		19 (3.2)	48 (3.4)
	Yuncker et al.	8404	Honduras	O		14 (3.0)	64 (2.9)
<i>B. platycarpa</i>	Klug	3040	Peru	O	P (UM '82)	24 (1.8)	68 (0.3)
	Klug	4116	Peru	O	P (UM '82)	27 (3.5)	67 (6.1)
	Pavon	s.n.	Peru	P	P (UM '82)	27 (2.8)	81 (7.9)
	Ruiz & Pavon	s.n.	Peru	P	P (UM '82)	15 (1.5)	77 (0.7)
<i>B. urucurana</i>	Fendler	328	Panama	—	U (DB '76)	29 (2.0)	52 (3.7)
	Garwood	1830a	Panama	O	U (NG '93)	42 (2.2)	117 (3.5)
	Garwood (J)	1830b	Panama	O	U (NG '93)	8 (0.8)	42 (1.9)
	Garwood (J)	1830c	Panama	O	U (NG '93)	10 (0.6)	48 (1.8)

	<i>Garwood</i> (J)	1830d	Panama	O	U (NG '93)	18 (2.1)	52 (1.0)
	<i>Garwood</i> (J)	2085c	Panama	O	U (NG '93)	7 (0.4)	51 (1.5)
	<i>Garwood</i> (J)	2085d	Panama	O	U (NG '93)	9 (1.1)	51 (1.6)
	<i>Garwood</i> et al.	613	Costa Rica	O	U (RD '94)	51 (4.0)	77 (4.7)
	<i>Khan</i> et al.	875	Costa Rica	O	U (RD '94)	42 (2.4)	81 (5.4)
	<i>Krukoff</i>	1069	Brazil	OU	U (RD '94)	64 (1.9)	101 (0.9)
	<i>Marshall & Neil</i>	6620	Nicaragua	OU	U (RD '94)	37 (1.3)	88 (6.9)
	<i>Philipson</i> et al.	1445	Colombia	O	U (UM '82)	61 (1.1)	110 (10.5)
	<i>Pittier</i>	4581	Panama	OP	U (RD '94)	50 (2.5)	110 (5.8)
	<i>Proctor</i>	32394	Honduras	OU	U (RD '94)	50 (1.3)	99 (5.4)
	<i>Rombouts</i>	177	Surinam	O	U (RD '94)	54 (1.9)	96 (9.5)
	<i>Schmalzel</i>	994	Panama	O	U (RL '88)	70 (5.6)	88 (8.5)
	<i>Seymour</i>	s.n.	Nicaragua	O	U (RD '94)	61 (5.0)	83 (5.8)
	<i>Triana</i>	s.n.	Colombia	S	U (DB '76)	56 (6.2)	116 (11.1)
<i>B. sp.</i>	<i>Garwood</i> (S)	2439a	Panama	?	U?(NG '93)	4 (0.4)	44 (1.7)

Original ID codes: A, *Bixa arborea*; E, *B. excelsa*; O, *B. orellana*; OO, *B. orellana* var. *orellana*; OU, *B. orellana* var. *urucurana*; P, *B. platycarpa*; S, *B. sphaerocarpa*; U, *B. urucurana*. Where original determinations have been confirmed or changed, this is noted in the 'Later ID' column, giving date and identifier: DB, D. Baer; UM, U. Molau; RL, R. Liesner; FR, F. Ramos; NG, N. Garwood; RD, R. Dempsey. Mean scale densities and diameters are calculated from 5 edge measurements on one leaf for all specimens except *Garwood* 1830a, b, e & d, 2089e & d, and 2439a, for which means include 10 edge measurements on each of two leaves. (J), juvenile specimen; (S), seedling; (SEM), standard error of the mean.

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